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Art. VI.—*A Disease of Cauliflowers in Victoria, Australia. (Gloeosporium concentricum (Grev.) Berk. and Br.).*

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(With Plate VI.)

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Introduction.

A disease of cauliflowers is very prevalent in Victoria, not only affecting the leaves, but also damaging the inflorescences, especially if heavy rains occur during the season. Affected plants greatly deteriorate in market value. The disease was brought under the writer's notice by Mr. D. Adam, Government Pathologist, Department of Agriculture, Victoria, in February, 1933. From communication with Mr. Adam the writer learns that a fungus resembling the Victorian pathogen has been isolated from *Brassica* leaves in England, and is considered to be a *Gloeosporium*. There exists no published account of this isolation.

The following account has been undertaken with the view of establishing the identity of the fungus isolated in Victoria, and of placing on record a detailed survey of the behaviour of the pathogen as it occurs on the host and in pure culture.

Symptoms.

The fungus occurs on the thick fleshy midribs, laminae, and petioles of cauliflower leaves, on both upper and lower surfaces (Plate VI., Fig. 1). The most characteristic feature is the presence of minute, roughly circular, greyish-white patches on both surfaces of the leaf. These are arranged in a more or less concentric pattern; each individual patch is the result of the fungus sporing beneath the cuticle of the host.

The formation of spores creates an internal pressure, which eventually ruptures the overlying cuticle. The spores then escape, and collect on the surface of the leaf in clusters; the latter are very white and fluffy, suggesting extremely minute fragments of cotton wool (Plate VI., Fig. 2). On the midribs and petioles these snow-white clusters of spores are not so easily seen, owing to the lack of contrasting green colour. However, brown to almost black scarred areas develop abundantly, usually after the spores have ruptured the cuticle. The scars are narrow, elongated in the direction of the course of the midrib, varying in length from less than 1 cm. to more than 2 cm., more or less raised at the margin, and slightly sunken towards the centre.

Small patches of brown discolorations may extend on to the laminae of the leaves, and are then found in the neighbourhood of the sporing areas. On the midribs and petioles the scars later become wrinkled or furrowed in appearance, owing to the formation of cork (Plate VI., Fig. 1).

Historical.

The genus *Cylindrosporium* was set up by Greville (9) in 1823, on the basis of *Cylindrosporium concentricum* Grev., found on both surfaces of cabbage leaves (*Brassica oleracea* Linn.). Greville stated, "The peculiarity of its cylindrical sporidia, and its situation on the surface of living leaves, fully entitle it to generic distinction."

In 1850, Berkeley and Broome (2) examined Greville's original material, and found that the spores were produced beneath the cuticle, and formed "little heaps by oozing out as in other species of *Gloeosporium*," and hence placed the fungus in this genus.

It is clear, therefore, that *C. concentricum* Grev. = *G. concentricum* Berk. and Br. Von Höhnel (16) in 1916 abandoned the old genus *Gloeosporium* as a mixture, and replaced it by four new genera, *Gloeosporina*, *Monostichella*, *Gloeosporidium*, and *Cylindrosporella*, of which the first two and the last had subcuticular acervuli, and in the third the acervuli lay deeper. *Gloeosporina* possessed micro-conidia. Nannfeldt (24) in 1931 showed that spore size was a very unreliable character, as acervuli may contain both macro- and microconidia, while others

may possess microconidia only; he suggested that *Gloeosporina* was founded in this way. He also regarded the attempt to divide the genera by their position in the host as futile.

In 1927, Karakulin(21) discussed von Höhnel's attempt to break up the genus *Glocosporium,* but he did not accept this suggestion in its entirety, owing to the lack of constancy in the morphological characters of the new genera. Karakulin regarded it as too early to abandon the old genus *Gloeosporium,* as it had widespread recognition, and no entirely satisfactory subdivision had, as yet, been proposed.

Since Greville's time, many species were placed, by Saccardo, under the genus *Cylindrosporium,* and a great deal of confusion resulted. Von Höhnel (17), however, in 1924, clarified this point. He discussed thirty-three species of *Cylindrosporium,* and referred these to eleven genera, five of the latter being new. Von Höhnel regarded *Cylindrosporium concentricum* as the only true species of the genus.

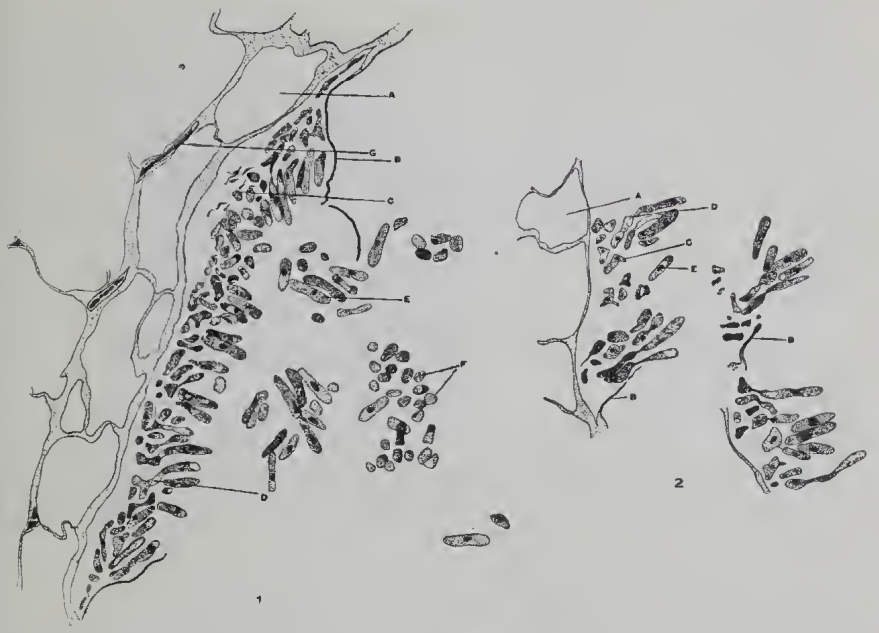
If Berkeley and Broome are correct, and the fungus is named *Gloeosporium concentricum* (Grev.) Berk. and Br., then there is nothing left in the genus *Cylindrosporium.*

Description of the Pathogen on the Host.

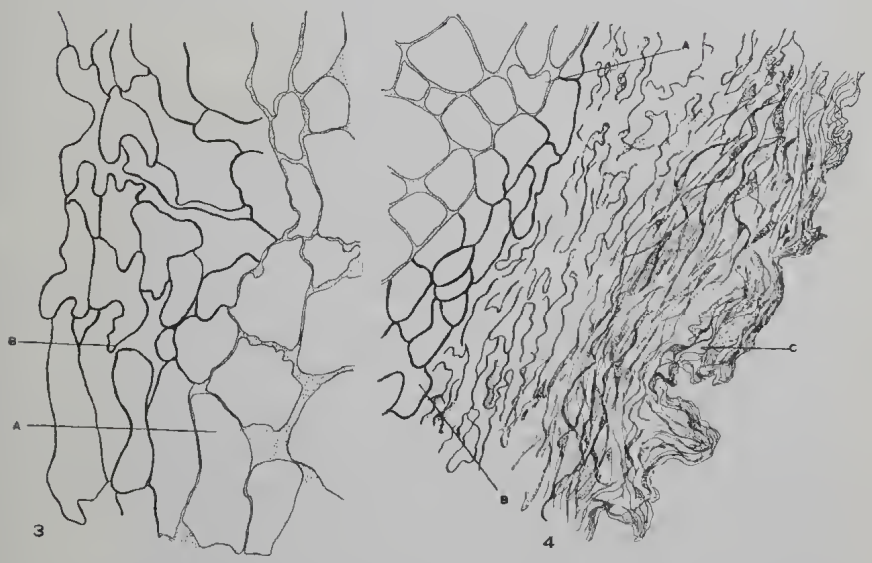
Spores of the fungus were easily obtained from the small snow-white fructifications on the leaves of the host, and were examined microscopically. They were extremely numerous, and each possessed a mucilaginous envelope. The spores measured on the average 11.9 × 3μ, and were cylindrical, rounded at each extremity, hyaline, straight, or slightly curved, one-celled, generally bi-guttulate, sometimes, however, more than one oil drop occurring at each end.

Portions of leaves of a diseased cauliflower were fixed, and embedded, and sections about 5μ thick were cut, and stained by Haidenhain's iron-alum haematoxylin method. In this way sections were obtained which showed the fructifications at a fairly young stage before the rupture of the cuticle, and a still later stage depicting mature fruiting areas when the cuticle of the host had been ruptured (Fig. 1).

The acervuli were subcuticular; intercellular fungal hyphae were observed within the leaf tissue, extending several layers below the cuticle (Fig. 1G). From a slight, but nevertheless well-defined stroma, the conidiophores arose perpendicularly. These were unbranched, fairly closely packed, short, usually one-celled, from which the conidia, each with a single well defined nucleus, were constricted off one at a time from the apex. One conidium was completely formed and set free before another started to develop (Fig. 2). The acervuli finally became erumpent, and the spores oozed out on the leaf surface.



FIGS. 1, 2.—1. Transverse section of an acervulus on the under surface of a cauliflower leaf. × 364. 2. Portions of transverse sections of acervuli, showing conidia borne on conidiophores. × 364. A. Epidermis of leaf; B. ruptured cuticle; C. stroma of acervulus; D. conidiophore constricting off a spore; E. spores set free; F. spores cut transversely; G. intercellular hyphae.



FIGS. 3, 4.—3. Transverse section through a midrib of a cauliflower leaf, at an early stage in cork formation. × 282. 4. A later stage showing the deep-seated cork cambium, and layers of diseased tissue. × 168. A. Cork cambium; B. cork cells; C. diseased leaf tissue.

Sections of midribs and petioles showing brownish-black scars were also cut and stained. They showed acervuli similar to those found on the laminae of the leaves. Sections of the scars after they became wrinkled in appearance showed a very extensive development of corky tissue, on the surface of which fungal hyphae were distinguishable, also a few spores. Early and later stages in cork formation are depicted in Figs. 3 and 4. Staining with chlor-zinc-iodine served to define the full extent of the corky tissue.

Description of the Pathogen in Culture.

(a) Isolation from Host, and Growth on Various Media.

The pathogen was first isolated from the leaves of *Brassica oleracea* in 1932, and since then frequent isolations have been made, and the fungus obtained in pure culture without any great difficulty.

The following media were used:—Malt agar, oatmeal agar, Brown's synthetic potato dextrose agar, cabbage agar*, sterilized cabbage midribs, sterilized potato slopes, turnip juice.

Malt agar (Plate VI., Fig. 3).—Growth is fairly slow and restricted. Young colonies have a puckered appearance with a moist cream-coloured mycelium, due to the formation of spores in great numbers. Later the culture turns dark green to black in colour, except at the growing edges, and small black spherical to sub-spherical bodies appear. These vary from 200μ–670μ in diameter, and may be simple or confluent. These structures appear macroscopically very like pycnidia. Ashby (1) in investigating *Gloeosporium musarum* states that, "Both Lasnier (22) and Toro (30) refer to these structures as pycnidia. Krüger calls them pseudopycnidia." The term was originated by Potebnia (25) when describing certain species of *Septoria*. Following Potebnia's example, the term pseudopycnidium will be used throughout this account.

A mature pseudopycnidium possesses a rounded or sometimes stellate ostiole, which opens wide to expose the hymenial layer of branched conidiophores bearing conidia.

Oatmeal agar.—Compared with the rate of growth on malt agar measured in terms of diameter of the colony, growth on oatmeal agar is quick. As the culture ages, the hyphae turn dark-green to black. On the dark mycelium, discrete sporing areas of a dirty cream colour, together with black spherical pseudopycnidia, are clearly visible. Aerial mycelium is absent in these cultures.

* 500 gms. of fresh cabbage leaves were boiled in 500 ccs. of water. The extract so obtained was made up to 500 ccs., added to 500 ccs. of 2 % agar plus 1·5 % dextrose, and autoclaved in Erlenmeyer flasks.

Brown's synthetic potato dextrose agar.—This medium is unfavourable to growth. The mycelium is slightly raised and very restricted, white to cream, and not moist, on account of limited spore formation.

Cabbage agar.—Growth on this medium is similar to that on malt agar. The pseudopycnidia, however, are not as numerous, and growth, on the whole, is more restricted.

Sterilized cabbage midribs.—On cabbage tissue the fungus exhibits a different mode of growth. The mycelium is more aerial in type. As the culture ages, there is a darkening of the tissue, and also of the fungal mycelium. Pseudopycnidia are developed.

Sterilized potato slopes.—This medium also exhibits a distinct type of growth. Young cultures appear quite dry, pure white, dense and decidedly wrinkled; later becoming black, accompanied by blackening of the potato tissue. Spore formation is very restricted and no pseudopycnidia are formed.

Turnip juice.—Growth in a liquid medium such as turnip juice is very slow, a mycelium is gradually formed on the surface. The spores may sink to the bottom of the tube, where they germinate.

It is evident, therefore, that starchy media, such as Brown's agar, and potato slopes, are unfavourable for the growth of this fungus; this was also noted by Lasnier (22) in his account of the growth of *Glomerella* (*Gloeosporium*) *Cattleyae* on starchy media.

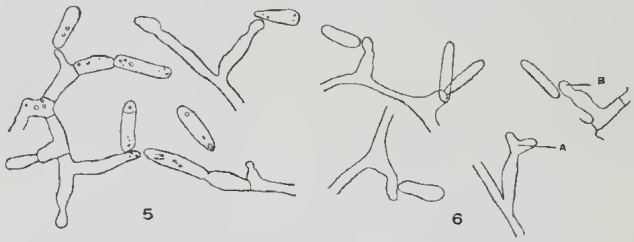
The optimum temperature for growth on any medium is from 19 deg. C.–20 deg. C., and all the cultures described above, were grown at approximately 19 deg. C.

b. Spore Production in Culture.

In culture the average spore measurements are as follows: 10.4–13.1μ $\times$ 2.5–2.8μ, and conidial formation takes place in three distinct ways:—

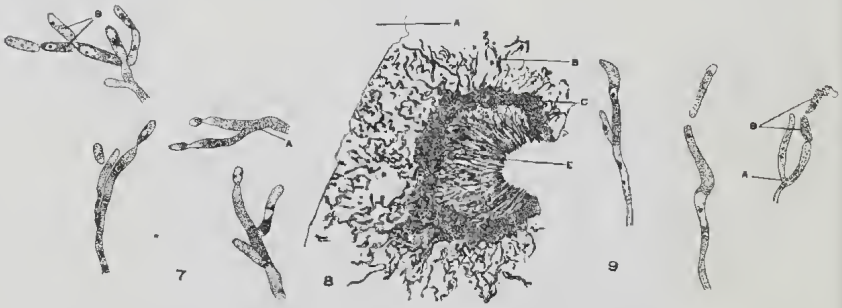
1. Conidia may be formed at any point throughout the culture; the conidiophores are short, branched, and arise from the ordinary growing hyphae. The conidia are constricted from the tip of a conidiophore, one by one; when one conidium is completely formed, it is set free, and then the conidiophore sends out a second spherical protuberance, which elongates until it reaches the normal dimensions of a spore, and is then set free. In this way numerous spores are formed from the one conidiophore, which is soon completely masked by them. This type of spore

formation is best studied in single spore colonies, which are sown in malt agar in petri dishes. Conidia commence to develop after about four days at 19 deg. C. (Figs. 5 and 6).



FIGS. 5, 6.—5. Colony grown on malt agar, from a single spore, showing conidia being formed at any point from short branched conidiophores, after five days. × 261. 6. The same after six days. × 261. A. Conidiophore commencing to divide into two; B. the second spore being formed, in succession.

2. The discrete sporing areas, which are easily seen on oatmeal cultures, are seen, when sectioned, to consist of a definitely raised plectenchymatous stroma, and from this arise numerous branched conidiophores, multicellular, elongated, and producing spores in the same way as described above. (Fig. 7.) On account of the well-developed stromata, these fructifications may be termed "sporodochia."

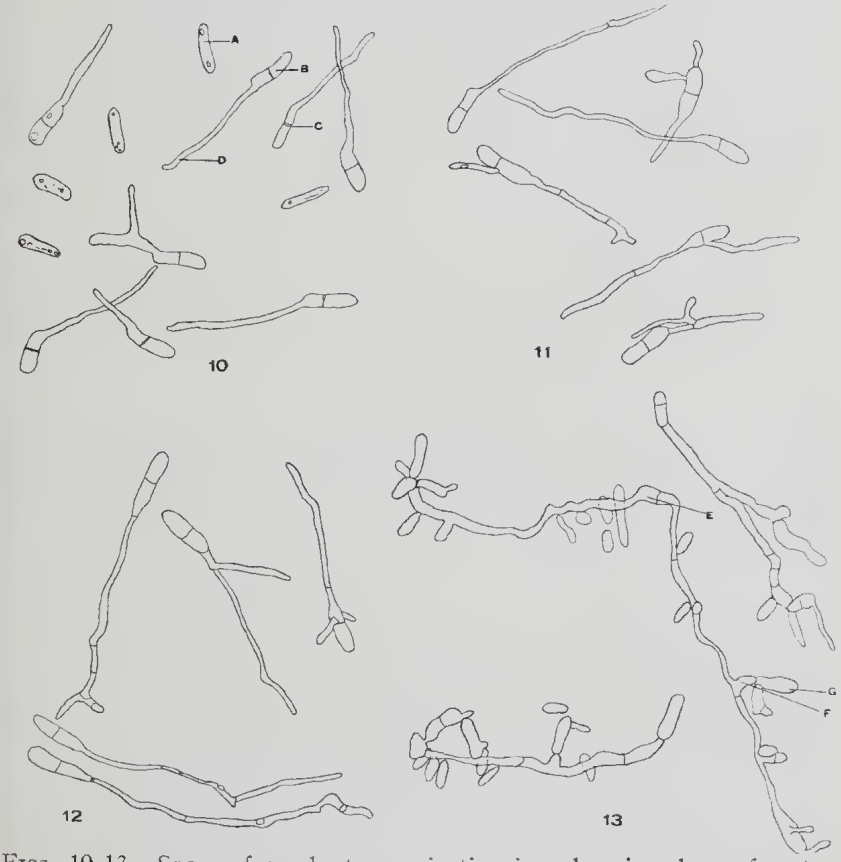


FIGS. 7–9.—7. Conidiophores and conidia from discrete sporing areas on oatmeal agar, from transverse sections. × 400. A. Elongated, branched conidiophore; B. conidia formed in succession. 8. Transverse section of a mature pseudopycnidium, growing on malt agar. × 43. A. Surface of culture medium; B. outer region of loose hyphae; C. dark inner region; E. elongated branched conidiophores. 9. Conidiophores and conidia from a pseudopycnidium. × 418. A. Branched conidiophore; B. conidia forming in succession.

3. Finally conidia are produced in pseudopycnidia. When sectioned a typical pseudopycnidium shows an outer region of loosely arranged hyphae, and a dark inner region, about 40μ in thickness, which consists of closely compressed hyphae. This inner region is lined by elongated, branched, conidiophores (Fig. 8), which produce conidia from their tips in the usual manner (Fig. 9).

c. Spore Germination.

This was studied in hanging drops of sterile water. Spores were germinated at 19 deg. C. and also at the fluctuating temperature of the laboratory. Germination commenced slightly earlier, and was more rapid at 19 deg. C. than at room temperature. The experiments were carried out with spores obtained directly from the host, and also with spores produced in culture.



FIGS. 10–13.—Spores from host, germinating in a hanging drop of water. × 291. 10. After 24 hours. 11. After 48 hours. 12. After 72 hours. 13. After six days. A. Conidium before germination; B. germinating conidium; C. medium septum in germinating conidium; D. germ tube; E. original conidium; F. conidiophore; G. secondary conidium.

After twenty-four hours spores about to germinate appeared slightly swollen, and others still further advanced showed a median septum. The first germ tube generally proceeded from one end of the spore, and later the other section of the spore produced germ tubes (Fig. 10). After forty-eight hours the germinating filaments exhibited septa, and some showed the commencement of branching (Fig. 11). Finally secondary conidia were produced from short conidiophores, as shown in Fig. 13, at or after six days.

Appressoria such as were observed in hanging drops of *Gloeosporium musarum* spores, were *not* formed by the fungus from *Brassica* leaves. The hanging drops were inverted, so that a great number of the spores when they germinated came into contact with the glass coverslip, thus receiving the contact stimulus necessary for the production of appressoria, but in no case were appressoria observed.

d. Chlamydospore production.

Chlamydospores were not noticed on actively growing cultures, but were frequently observed in very old cultures and were abundantly developed on Brown's agar. The chlamydospores measure from 10–15μ × 5–9μ, and may be developed either in an intercalary position or terminally. (Fig. 14.) They are roughly oval to round in shape, and pale yellow in colour.

Inoculations to prove Pathogenicity.

Healthy cauliflower seeds were planted in seed boxes, and when the plants had grown about three inches high, they were transplanted into small flower pots, one plant in each pot, and allowed to establish themselves.

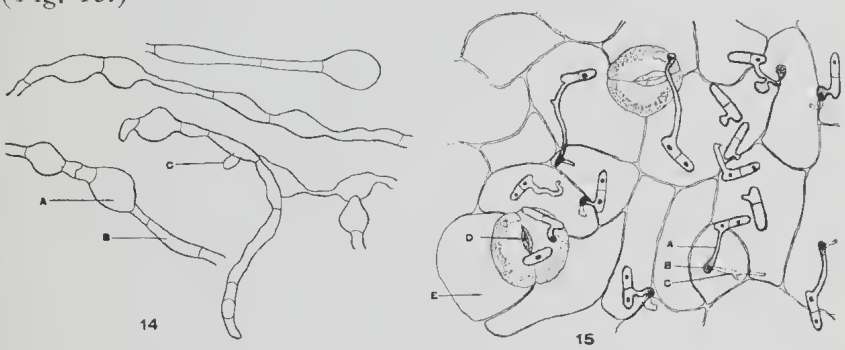
Then four plants were sprayed with a suspension of spores in distilled water and controls with distilled water alone. The seedlings were placed in a glasshouse and kept in a moist atmosphere for four days. Then they were placed under ordinary glasshouse conditions, and the plants closely examined each day for the first sign of infection.

After ten days minute blackish scars were noticed on the stems of the infected plants. At this stage the pots were transferred to a sheltered position out of doors.

Later the small scarred areas extended up the midribs of the leaves and along the veins. Spores were easily demonstrated from stems or leaves, occurring in the characteristic snow-white areas, associated with the darkened regions. (Plate VI., Fig. 4.) Symptoms were developed by each of the four infected plants. The control plants showed no sign of infection, remaining healthy throughout the experiment. The above experiment was repeated with the same results. The pathogen was isolated quite readily from the sporing areas on the leaves or stems of the seedlings, and its appearance on culture media agreed in every particular with the growth of the fungus isolated from diseased plants in the field.

In order to determine the way the pathogen entered the host, seedling leaves of cauliflowers were sprayed with a spore suspension and the plants treated as before. After four days, the leaves were removed from the plants, and fixed in Gilson's fixative, then stained with cotton blue in lacto-phenol for about an hour. When examined microscopically the spores with their germ tubes were stained a deep blue, the single cross wall in each germinating

spore was clearly defined. The germ tubes seemed to penetrate the leaves more readily on the lower surface, and in many instances just at the point of penetration the filament seemed to swell slightly, but in no case was a definite appressorium developed. The germinating filaments, after piercing the cuticle, could easily be traced for some distance, appearing a paler blue colour, owing to the overlying cuticle. Germ tubes entered the leaf through the walls of the epidermal cells and the guard cells, but were not found passing through the stomatal pore in any case. (Fig. 15.)



FIGS. 14, 15.—14. Chlamydospores developed on Brown's agar. × 282. A. Chlamydospore; B. hypha; C. conidium. 15. Spores germinating on the under surface of a cauliflower leaf, after a period of 4 days. × 282. A Germ tube on surface of leaf; B. point of penetration; C. germ tube after penetrating cuticle; D. stomatal pore; E. epidermal cell of leaf.

The Effect of pH on Spore Germination.

The effect of various pH values on spore germination was tried. Hanging drops over a wide range of pH values were set up in sterile water, with spores obtained directly from the host. The hanging drops were placed in a moist atmosphere, and left at room temperature for 24 hours. The maximum temperature during this period was 14.4 deg. C., and the minimum 10 deg. C. Spores in sterile water (pH 6.0) were used as controls.

The percentage germination at each particular pH value was determined after taking counts from five microscope fields. The results are tabulated below:—

Spores Germinating in Lactic Acid.		Spores Germinating in Na_2CO_3.	
pH.	Average Germination.	pH.	Average Germination.
	%		%
4·9	62	8·4	75
3·9	73	9·4	73
3·7	39	9·6	67
3·5	35	9·9	74
3·4	32	10·1	61

The controls gave an average percentage germination of 95.5 per cent. On each side of pH 6 a general fall in percentage germination of spores took place, from 95 to some 73 per cent., within a range of pH 9.9 and 3.9. Beyond this range the percentage germination fell sharply, especially on the acid side.

Discussion.

In 1823, Greville described a fungus from *Brassica* leaves in Scotland, which he named *Cylindrosporium concentricum*. Later Berkeley and Broome examined Greville's original material, and changed the name to *Gloeosporium concentricum* (Grev.) Berk. and Br. Buddin, whose work is unpublished, isolated a fungus in England which (Miss) Wakefield considered to be undoubtedly *Gloeosporium concentricum* (Grev.) Berk. and Br.

The average spore measurements of the fungus found on *Brassica* leaves in Victoria are $11.9 \times 3\mu$. Buddin's spore measurements for his fungus are $10 \times 2\mu$. The latter show a good practical correspondence with the measurements obtained for the Victorian pathogen. The spores are not very narrow in relation to their length, and come well within the range of spore measurements for a typical *Gloeosporium* species. The way the conidia are borne on the ends of short conidiophores, in this case usually unbranched in the acervuli, is also typical of *Gloeosporium*. The type of spore formation when compared with that of *Gloeosporium musarum* is found to agree in every particular. A typical *Gloeosporium*, however, generally develops appressoria, when the germinating filaments are stimulated by mechanical contact. The greater number of diseases described as anthracnoses fall under the genera *Gloeosporium* and *Colletotrichum*, and in the majority of these appressoria are developed. However, both on the host and in hanging-drop cultures of water, appressoria fail to develop in the fungus under discussion. It is usually considered that a genuine *Gloeosporium* develops subepidermally, whereas this fungus originates subcuticularly. It has been mentioned above that Naumfeldt regards the attempt to classify genera by their position within the host (subcuticular, subepidermal, &c.) as futile. The perfect stage of the fungus has not been found, as yet, on the host or in culture. Many methods of culture have been tried, in order to try and induce the perfect stage, but up to date without success.

From the data collected, it is evident that the lack of appressoria is the only real divergence from *Gloeosporium*. Correspondence with Butler reveals the fact that it is uncertain whether Greville's fungus and that isolated by Buddin are the same species. Butler suggests that until Greville's fungus is redescribed the name *Gloeosporium concentricum* (Grev.) Berk. and Br. may stand.

The form isolated in Victoria seems to resemble Buddin's isolation. Therefore, until the redescription of Greville's fungus and the discovery of a perfect form, Butler's suggestion is followed—the Victorian pathogen is retained in the Melanconiaceous genus *Gloeosporium*, the full nomenclature being *Gloeosporium concentricum* (Grev.) Berk. and Br.

Summary.

1. A study of a disease of cauliflowers in Australia has been made, as a result of which the pathogen is named *Gloeosporium concentricum* (Grev.) Berk. and Br.

2. A disease was recorded on *Brassica* leaves in Scotland by Greville in 1823, when he considered the pathogen peculiar enough to entitle it to generic distinction—hence he named it *Cylindrosporium concentricum* Grev. Berkeley and Broome, in 1850, examined Greville's material, and changed the name to *Gloeosporium concentricum* (Grev.) Berk. and Br.

Buddin isolated a fungus in England which Wakefield considered to be *Gloeosporium concentricum* (Grev.) Berk. and Br. However, Butler is uncertain whether Greville's fungus and that isolated by Buddin are the same species, and suggests that until Greville's fungus is redescribed, the name *Gloeosporium concentricum* (Grev.) Berk. and Br. may stand.

3. The disease is characterized by minute snow-white clusters of spores, which burst through the cuticle of the leaves and stalks, the sporing areas or acervuli being arranged more or less concentrically.

4. The pathogen was isolated from the host, and obtained in pure culture. Growth on different media was studied.

5. Spore germination was followed in hanging drops of sterile water, and the effect on germination of varying pH values was studied.

Acknowledgments.

The author wishes to record her appreciation of the helpful interest of Professor Ewart, and to thank Dr. McLennan, under whose guidance the work was done. Gratitude is also expressed to Dr. Butler of the Imperial Mycological Institute, for his valuable suggestions.

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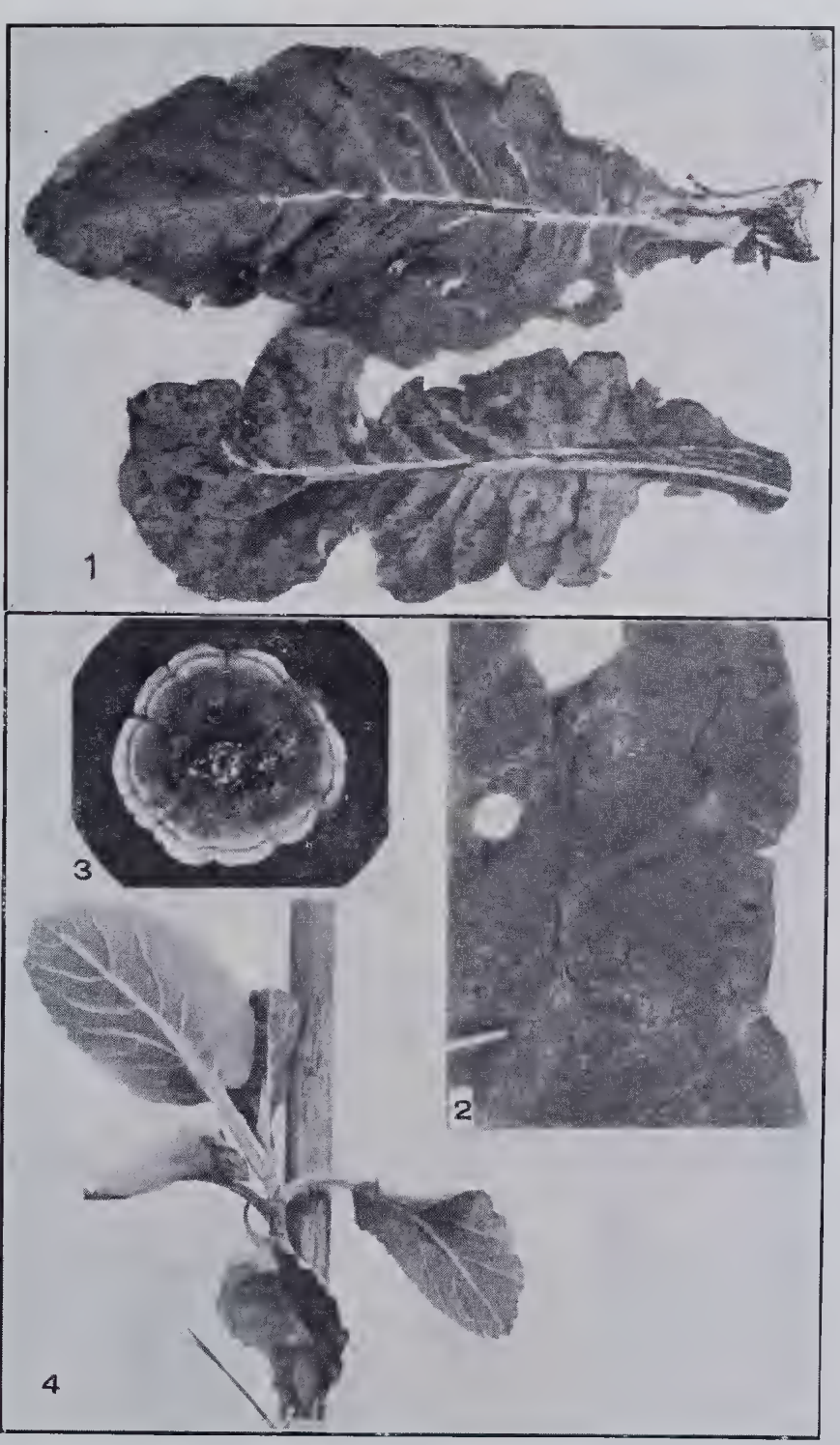

Gloeosporium concentricum on Cauliflower.

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Explanation of Plate VI.

Fig. 1.—Cauliflower leaves infected with *Gloeosporium concentricum*. Note the white sporing areas associated with the blackened regions on the laminae, and the corky scars on the midribs.

Fig. 2.—Portion of a cauliflower leaf infected with *Gloeosporium concentricum*, showing the white fructifications somewhat concentrically arranged.

Fig. 3.—*G. concentricum*, growing on malt agar. Note small black pseudopycnidia, blackened stroma, and white growing zone.

Fig. 4.—Cauliflower seedling, which developed symptoms of the disease after being sprayed with a spore suspension of *G. concentricum*.